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PITCH PERCEPTION

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ABSTRACT

This paper is a comprehensive review of auditory theory and research that bear directly or indirectly on pitch perception. It considers pitch perception from three major points of view. First, it reviews the history of pitch-perception studies and describes some representative theories of hearing they have engendered. Second, this paper examines various auditory phenomena in the light of how well the different theoretical positions can explain them. Finally, it attempts to collate physiological and anatomical findings about the auditory nervous system and, again, use the facts which emerge to test the adequacy of theoretical concepts and explanations. The 213 references include studies of both humans and animals.

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PART I: HISTORY OF PITCH PERCEPTION

INTRODUCTION

The present paper is an attempt to review, analyze, and integrate the literature of pitch perception. It assumes that hearing is a problem for psychology because the accurate measurement of what men and animals discriminate about sounds is simultaneously a definition of the phenomena for which neuroanatomy and physiology are to uncover neural correlates. When the findings of neuroanatomy and neurophysiology are adequately integrated, the results should be a simple, logical, and adequate set of neural correlates for explaining auditory experience.

It is interesting to point out that the problems of pitch perception are unique to men, for no other animal can describe his subjective experiences as he listens to a single tone or call one tone "higher" than another in pitch. The primary challenge for psychologists is to present an adequate explanation of the transduction of physical vibrations into the experience of tone. Furthermore, if two pure tones are presented in succession, two different pitch perceptions emerge. The mechanism which detects slight physical differences in the sound needs to be determined. Finally, listening to two tones sounding together presents another problem. Physically, such a stimulus is a single complex wave, and we usually hear it that way. Yet we may choose to attend to one of the tones and ignore the other. How is the complex wave analyzed into its simple components, and how, furthermore, does the auditory system suppress one product of the analysis and not others?

These and a whole host of other problems are related to the perception of pitch, and the present paper is a review of the psychological, physiological, and neuroanatomical studies which attempt to determine the mechanism of pitch perception. Structurally, the paper is divided into three parts: the history of pitch perception, auditory phenomena, and physiological, sensory, and central processes in pitch perception.

"Pitch perception is the qualitative aspect of auditory experience which extends in a continuum from the lowest audible to the highest audible tones" (199). In other words, pitch is one means for distinguishing and classifying auditory sensations. Designating high-frequency tones as <u>high</u>-pitched tones and low-frequency tones as <u>low</u>-pitched tones, by words meaning <u>high</u> or <u>low</u> appears to have some basis in phenomenal experience. When subjects (<u>S</u>s) are asked to localize the apparent source of tones produced behind a screen, they attribute a higher locus to the high-pitched tones than to the low ones, even though the actual source of the tones remains unchanged (140).

Limits of Pitch Perception

Although 20 and 20,000 cycles per second (cps) are often referred to as the limits of pitch perception, this does not mean that nothing is sensed below 20 cps or above 20,000 cps. Tonal pitch has been reported to occur quite suddenly at 18 cycles. The lower frequencies result in auditory sensations of a complex, noisy character. The sound is made up of numerous components of rather high frequencies estimated as well over 1000 cps. Interestingly enough, as the stimulus frequency is varied downward from the region of 15 cps, the pitch of the noise pattern appears to rise. Audibility extends at least to five cps, and Bekesy (16) has reported observations down to one cps. The lower limit for pitch is difficult to determine with precision because of the difficulty of distinguishing between a very low frequency heard as a tone and one which is heard as a series of distinguishable pulsations; and the ear itself introduces distortion (aural harmonics) at low frequencies, so it is difficult to discriminate between the fundamental tone and the higher harmonics (173).

Frequency-Intensity Relationship

Pitch is determined by the direct response of a human observer to a sound stimulus, whereas frequency is a parameter of the physical stimulus. Physicists have generally used the two words interchangeably, on the false assumption that experienced pitch is solely determined by the frequency of the stimulus. Thus Barton (14) in his treatise on sound, says, "The pitch of a musical sound. . . depends upon the period or frequency of the vibrations constituting the sound and upon that alone." Many investigators (60, 113, 126, 167, 173, 183, 199, 212) have noted that the pitch of a tone seems to change when its intensity changes -- for example, when S is required to reproduce vocally the pitch of a tuning fork (middle C). When the fork is held close to the ear so its intensity is increased, the pitch of the singer's voice is slightly lower (126). That is, the S hears the louder tone as lower. Also, Stevens (171) has found that pitch decreases with intensity; but, for high tones, pitch increases with intensity. For certain tones in the middle range (e.g., 2,000 cps), pitch remains the same, regardless of loudness.

Here we have a phenomenon resembling the Bezold-Brucke effect in vision, where changing the intensity of a visual stimulus produces a change of hue. The analogy holds even further, however, for just as there are frequencies at which pitch does not vary with intensity, so likewise hues at certain wavelengths of light remain the same even when intensity varies.

The intensity-frequency relationship and the threshold of hearing will be discussed at greater length later on, but it should be evident by now that the perception of pitch is by no means a simple problem. We will now turn our attention to the history of pitch perception so that we may gain a perspective for examining the present Zeitgeist of auditory research.

CLASSIFICATION OF THE THEORIES OF HEARING

The history of pitch perception is also the history of the theories of hearing, because the latter have attempted almost exclusively to explain how we perceive pitch. However, a theory of hearing must not be limited to explaining pitch perception, but must also include explanations for the psychological variables -- loudness, timbre, and related experimental auditory phenomena.

There are two main types of pitch theories. One division assigns the perception and discrimination of pitch to a specific locus in the cochlea. These are the "place theories." They subdivide further according to whether they accept or reject the resonance principle. In contrast, the "frequency theories" assume that the frequency of the mechanical vibrations is communicated to the auditory nerve and then transmitted to the higher nerve centers. According to frequency theory, this frequency, as centrally represented, provides the basis for pitch perception. Furthermore, these theories may be subdivided into two groups by whether or not they accept the principle of peripheral analysis.

Although there are many more theories of hearing than this paper will present, each theory presented will represent a unique approach to explaining the perception of pitch. For a more detailed historical treatment of pitch perception, see Wever (199) and Wever and Lawrence (203).

Beginnings of Auditory Theory

The earliest known theory of sound perception is that of "aer implantus," suggested by Aristotle in the fourth century, B. C. (160). The theory assumed that, since sound results from an airborne impulse, it required a cavity in the head filled with air to respond to the impulses originating in the outer air. This air, implanted during uterine development, was the actual end organ of hearing. However, in 1760, Cotugno (33) discovered that the labyrinth of the ear is filled with fluid, not with air. Numerous concepts were proposed about structures, supposedly existing in the internal ear, which should respond to sound impulses by vibrating. Some investigators believed that "sonorous bands," stretched across the cavity of the cochlea, were set into vibration. In 1680, Perrault (141) proposed that there exists in the cochlea a vibrating mechanism which responds to impulses of tone waves. DuVerney (55), in 1683, likened the cochlea to a musical instrument with different parts responding to tones of different pitch according to the principles of physical resonance. He assumed that the lamina spiralis was the vibrating mechanism and, since this bony plate is broader in the basal coil and becomes gradually narrower towards the apex of the cochlea, he located perception of low tones in the basal coil and of higher tones in the apex (162).

Scarpa (156), in 1798, discovered the membranous labyrinth, and Corti (32), in 1851, discovered the details of the end organ in the cochlea, which now bears his name. As a result of these discoveries came the conviction that the anatomical structure is the hair-bearing cell which receives the terminal filaments of the acoustic nerve. Thus the problem of sound perception was reduced to determining the manner in which these hair cells are activated. Helmholtz (87), the great physicist, adopted as the method of stimulating the hair cells, the principle of physical resonance, which had formed the basis of theories for at least 200 years before his time.

Helmholtz's Resonance Theory

Thus, the era of modern auditory theory began in 1857 with the introduction of Hermann L. F. Helmholtz's first formulation of his resonance-place theory (87). The theory was presented in his magnum opus, Die Lehre von den Tonempfindungen. His theory was enthusiastically accepted, because it was presented along lines of musical harmony and musical perception, thus illuminating a field of popular interest. Furthermore, the theory was related to three important scientific discoveries of his time.

Helmholtz believed the ear analyzed sounds in accordance with Ohm's law of the analysis of complex sounds (135). The exact statement of Ohm's law of auditory analysis is that the ear performs the type of analysis defined by Fourier's theorem (66). For example, if someone sounds a complex note whose fundamental frequency is 1000 cps, we should be able, after training, to recognize not only the 1000-cps component but also the overtones at frequencies of 2000 cps, 3000 cps, 4000 cps, and so on. This phenomenon served as conclusive evidence for Helmholtz's argument of selective resonators in the ear.

In his Handbuch der Physiologie, Johannes Mueller (128) presented his now-famous doctrine of "specific energies," which has greatly influenced theories of sensory processes, especially hearing. The doctrine attempted to resolve the ancient problem of our sensory phenomena and their relation to the external world. His principal statement was that "sensation consists in the sensorium receiving through the medium of the nerves, and as the result of the action of an external cause, a knowledge of certain qualities or conditions, not of external bodies, but of the nerves of sense themselves" (128). In other words, there is a specific nerve corresponding to each sense; and one nerve can determine only its own kind of sensation. Mueller (128) did not indicate the precise location of the origin of sensory quality in the nervous system.

Helmholtz (87) not only adopted Mueller's doctrine of specific energies for his theory of hearing, but extended the doctrine to explain pitch perception within the sensory modality. That is, specific fibers exist which are tuned to respond to a particular frequency (tone). Helmholtz accepted this extensive multiplication of auditory specificities; and his resonance theory was an attempt to indicate concretely the nature of the processes, physical and physiological, on which these specificities depend.

Influenced by Corti's (32) anatomical work, Helmholtz assumed that the outer rods of Corti were the actual resonators, because they seemed to be under tension, and because they had their "feet" on the free, movable part of the basilar membrane. Following this assumption, Helmholtz argued for a series of progressively tuned resonators in the ear, with high tones located at the base of the cochlea and low tones at the apex.

Carefully measuring the cochlear structures, Hensen (88) pointed out that the outer rods of Corti vary in length only about twofold throughout the entire extent of the cochlea, far short of the range of resonance characteristics required for hearing several octaves of tones. He suggested that the basilar membrane, which varies about twelve-fold in width from base to apex, would be a more appropriate resonant structure.

In addition, Schultze (159) pointed out that the auditory nerve fibers do not terminate upon the arches of Corti but upon the hair cells. This observation, combined with Hasse's finding that the arches of Corti are not found in birds, forced Helmholtz to turn to the transverse fibers of the basilar membrane as the resonators (86).

Thus Helmholtz believed that the analysis and synthesis of complex sounds could be explained by a system of resonators in the ear, and on no other basis. If this assumption is to be verified, the ear must function with the properties of a resonator and operate in accordance with the physical laws and limitations of resonator action.

One condition of resonator action that Helmholtz specifically considered was the degree of independence of the resonators in the ear. Although the transverse fibers of the basilar membrane are not separate and free, but are embedded in the matrix of the membrane, Helmholtz believed that because the transverse tension is great and the longitudinal tension is "vanishingly small," independence of the fibers can be assumed (134, 185).

A further requirement of Helmholtz's theory is that the resonators be graduated in characteristics corresponding to the range of discriminable pitches. Thus the graduation of the resonators corresponding to the range of discriminable pitches was based on the progressive variation in the length of the transverse fibers of the basilar membrane.

Lastly, if the sensations of pitch arise separately and independently in the action of the cochlea, then there should be a resonant element for every discriminable tone, and the total number of elements should be at least as large as the number of distinguishable tones in the audible range. Helmholtz correlated Kolliker's (105) reports of the number of rods of Corti with Weber's measurements of pitch discrimination. Kolliker had found about 3000 rods of Corti in the human cochlea. Helmholtz assigned 200 rods of Corti to the "non-musical" ends of the scale where discrimination is poor, and the remaining 2800 to the middle seven octaves where discrimination is highly accurate.

However, Weber had demonstrated that experienced musicians can discriminate tones of 1000 and 1001 cps, or about 64 steps in a single semitone, so there were about twice as many discriminable pitches as available elements. Helmholtz surmounted this difficulty by arguing that a tone at a frequency midway between the tones proper to two adjacent rods of Corti will affect both of them at once; and this kind of action will be interpreted perceptually as a tone of intermediate pitch. Thus we hear a steadily rising frequency as continuous in pitch, rather than ascending by discrete steps.

Even though Helmholtz assumed the transverse fibers of the basilar membrane were the resonators, he still maintained his belief in the importance of the arches of Corti. The arches of Corti were assigned the role of intermediaries between the resonating basilar membrane fibers and the auditory nerve terminations. Thus the arches were affected by the movements of the basilar membrane fibers, and then they communicated the effects to the hair cells.

Finally, when Helmholtz tackled the question of the selectivity and persistence of the cochlear resonators he concluded that ". . .when we hereafter speak of individual parts of the ear vibrating sympathetically with a determinate tone, we mean that they are set into strongest motion by that tone, but are also set into vibration less strongly by tones of nearly the same pitch, and that this sympathetic vibration is still sensible for the interval of a Semitone" (87). Although Helmholtz did not emphasize this point, he failed to see that, when the resonators no longer act separately, they cease to obey the law of specific energies.

Helmholtz's theory dominated the field of audition for many years, but in 1886 Rutherford (155) attacked the basic concept of peripheral analysis and proposed an alternate theory of hearing. Emerging doubts about the presence of "stretched strings" in the ear, as well as the rejection of the place principle, eventually led to the substitution of a new "frequency" principle of nervous representation.

In view of existing evidence, Helmholtz's resonance-place theory is subject to a number of criticisms. First, the human ear is capable of perceiving pure tones between 20 and 20,000 cps, roughly a 10-octave range. However, the fibers of the basilar membrane, on the basis of variation in size, can account for only a three-octave range (136).

Secondly, Helmholtz assumed that the basilar membrane is under tension. Bekesy (17), by direct observation, has proved that the basilar membrane is not under tension.

The auditory perception elicited by a single tone is pure, not fuzzy. How is this possible, given the interconnectedness of the fibers along the basilar membrane? Gray (83) argues that by some unexplained mechanism the less intensely excited, bordering elements are inhibited and only the pitch corresponding to the locus of maximal stimulation is experienced. This problem has been a "thorn in the side" of Helmholtz's theory, and still needs an adequate explanation.

When Helmholtz formulated his theory of hearing, nerve physiology was in its early stages of development. Thus, after representing pitch by the particular nerve fibers actuated in a given case, he seemed to correlate intensity with the strength of the nerve process involved; in fact, Helmholtz hardly more than hinted at the correlation. (However, it is pertinent to point out that adherents of the telephone theory are equally at fault in omitting an explanation of intensity.)

The problem of intensity in audition came into prominence (7, 24) following the discovery of the all-or-none characteristic of muscle and nerve response. If a nerve fiber, once stimulated, always responds with a vigor that is a function of its own condition, not of the strength of the stimulus, then the simple straightforward explanation of intensity is no longer tenable.

Forbes and Gregg (65) have treated the implications of the all-or-none principle for auditory theory and revamped the Helmholtz resonance-place theory to make it consistent with this principle. According to them, pressure-variations of an auditory stimulus are transmitted to the cochlea, and there excite limited portions of the basilar membrane through resonance. Analysis of complex wave-forms is considered to be a peripheral process. The place of excitation on the basilar membrane represents frequency of stimulation and, consequently, pitch perception is a function of the particular nerve fibers excited.

According to the theory, intensity is determined by the number of impulses in the nerve response. The number of impulses can increase if there is an increase of neural activity in the fibers concerned, or an increase in the number of fibers acting, or by both these methods. A greater amplitude of sound waves produces a greater amplitude of movement of the portion of basilar membrane involved. Amplitude of movement is then transduced into excitation process, and the increased magnitude of this process presumably leads to an increased frequency of response in the nerve fibers concerned.

The second means of explaining intensity assumes that a greater sound-wave intensity produces a greater spread of response on the basilar membrane, resulting in excitation of more nerve fibers. This problem has been discussed previously under the topic of Gray's principle of maximum stimulation (83).

Even the fact that Helmholtz's theory is subject to severe criticism does not detract from the genius of the man, for he provided "much food for thought" for the years that followed.

Ewald's Pressure-Pattern Theory

Ewald's (58) pressure-pattern theory, as well as those of Hasse, Shambaugh, and Wever (86, 161, 199) are generally classified as the membrane-resonance theories. Basically, these theories reject two of Helmholtz's assumptions: transverse tension on the basilar membrane, and the negligible restraint that the cross connections of the membrane impose on the fibers' independent movement. However, they retain the principle of resonance.

J. R. Ewald (58), a physiologist, rejected resonance of specific elements as well as the notion of a broad local response of the tectorial membrane that Hasse (86) proposed. Ewald believed that stimulation threw the basilar membrane into general and extensive vibratory patterns. These patterns -- or "acoustic images" as Ewald called them -- were unique for every discriminable sound.

The "acoustic images" result from standing waves on the basilar membrane. Ewald conceived of waves traveling over the basilar membrane from base to apex, then reflecting back to the base. Such an action will create standing waves similar to the ones produced in a cord when one end is secured and the other end is moved up and down rapidly. Portions of the cord will be in vigorous up-and-down movements while others remain at rest; these portions are called loops and nodes respectively. Furthermore, the number of loops and nodes, as well as the distance between the nodes, depends on the frequency of vibration. Ewald conceived of the basilar membrane as acting like a cord, except that it is anchored at both ends and movement results from energy communicated to its midportion.

The spatial separation of the loops, which is large for low tones and becomes progressively smaller for high tones, serves as the cue for pitch perception. Ewald's theory thus avoids the physical and anatomical liabilities of specific independent resonators. Furthermore, Ewald localized high tones in the basal region of the basilar membrane, although he assumed low tones were distributed over the entire membrane. The theory explains noises as the absence of fixed patterns and the formation instead of moving, ever-changing patterns.

Observations from the "camera acustica," consisting of a thin rubber membrane stretched over a wedge-shaped opening in a block, provided experimental support for Ewald's theory. Excitating the membrane with a vibrating tuning fork produced a pattern that varied with the frequency of the sound but was constant for any given sound. Lehmann (110) criticized these demonstrations, maintaining that the patterns were "optical illusions" determined by the particular way the membrane was illuminated during its vibration. He found complicated patterns, largely restricted to one region. In addition, Lehmann suggested that the breadth, tension, and stiffness of the basilar membrane determine the regions that move in response to particular frequencies.

The advantage of the membrane-resonance theories is their relatively simple assumptions about the physical properities of the membrane. The only requirement for the basilar membrane is that the response vary significantly for different sounds. The cue for pitch perception and discrimination is a very simple one: the spatial separation of stimulated areas. However, the membrane-resonance theories (particularly Ewald's) fail to provide an adequate explanation of the analysis of complex sounds. It is difficult to comprehend separating several patterns which are present simultaneously. Other comments might be made about the details of the Ewald theory, but they will not be developed here.

Another variation of "place theory" is the non-resonance place theories or the "traveling-bulge theories," which postulate a progressively moving wave of displacement on the basilar membrane. Theories of this type were proposed by C. H. Hurst (96), E. ter Kuile (107), and H. J. Watt (195).

Traveling-Bulge Theory: ter Kuile

Turning our attention to Emile ter Kuile's theory (107), we find it is based on the idea of unidirectional wave motion in the cochlea. For ter Kuile, pitch perception depends upon how far up the cochlea this wave motion extends. Accordingly, when the stapes moves inward from its most outward position, it displaces fluid that makes the basilar membrane bulge downward. This bulge, beginning at the extreme basal end of the membrane, is immediately propagated toward the apex of the basilar membrane. Propagation is a function of the elastic properties of the membrane and the discrepancy between the amount of fluid displaced and the flexibility of the basal portions of the membrane. When the stapes reaches its most forward position, the bulge attains its greatest length. However, when the stapes is retracted, the bulge is erased.

The perception of pitch, then, is a function of the distance of the basilar membrane excited, measured from the basal end to the farthest point reached at the moment the bulge disappears. The length of this excited portion of the membrane depends on the period of the wave, which varies inversely with the frequency; the low tones will excite a larger portion of the basilar membrane than high tones. However, it is the entire portion of the membrane stimulated that provides the cue for pitch perception, rather than an isolated point of stimulation.

For ter Kuile, stimulating the entire basilar membrane in an irregular fashion produces the perception of noise. Furthermore, his theory accounts for low-frequency hearing loss following apical cochlea damage, as well as for the perception of pitches in a continuous series from high to low.

Meyer (124) objected to ter Kuile's assumption that the basilar membrane is elastic and that a bulge formed on it is propagated forward by virtue of this elasticity. Secondly, if the cue to pitch is the length of the stimulated path, injury to the apical elements of the cochlea should not cause a disappearance of all response to these tones. In fact, the low tones should stimulate all the elements remaining, and consequently all frequencies below some point should sound alike. Lastly, it seems untenable to essentially dismiss the return phase of the stapes' reciprocal movement. See H. J. Watt (195) for a further elaboration of ter Kuile's theory.

A theory of hearing that initially took the form of a traveling-bulge theory was proposed by Georg von Bekesy (15) in 1928. Working with models of the cochlea similar to those used by Ewald (58), Bekesy found that, by varying the thickness of the rubber film, the response to a tone could be restricted to a narrow region or even to a sharply defined spot. Continuing this line of investigation with specimens of human and animal cochleas, he reported that the forms of movement that were revealed agreed with those that had been observed in the mechanical models. Because of technical difficulties, he made the majority of his observations near the apical end of the cochlea (19).

Bekesy, then, was able to infer the forms of the traveling waves throughout the cochlea. He located the point of maximum stimulation for high tones in the basal portion of the cochlea, and for low tones toward the apex, just as Helmholtz did. Thus the effects of all tones are distributed over the cochlea in a manner that varies systematically with frequency. The perception and discrimination of pitch depend upon this distributed action.

Bekesy (19) also studied the phase relations among the cochlear structures. For the low tones, he found that there is complete phase agreement in all the moving parts at the exposed position; the tectorial membrane, the organ of Corti, the basilar membrane and usually Reissner's membrane also undergo vibratory movements as a whole. However, as the frequency rises, a notable lag appears and this lag increases rapidly as the wave moves up the cochlea. Bekesy argued that this sort of phase variation indicates that we are dealing with traveling waves whose wavelengths grow shorter as the frequency rises.

Bekesy believed that the differentiation of cochlear action with frequency is the result of properties of the dividing partition (200). Measurements were made on various parts of the partition to determine their differential stiffness. Pressure was applied to various regions of Reissner's membrane, the tectorial membrane, the organ of Corti, and the basilar membrane, and the resulting depressions were observed. He found that the stiffness of the basilar membrane varied about 50-fold between the 10mm and the 30mm positions; this was the only area of the cochlea that varied systematically. Though its resistance to displacement varies, this membrane is not under tension; rather, it is a fairly uniform, unstressed plate (19).

Bekesy believed that, just on the apical side of the point where the amplitude of the traveling wave is largest, the undulations of the basilar membrane cause an eddy movement on either side of the membrane. He suggested that this eddy movement, which is much more restricted in scope than the wave motion as a whole, caused the actual excitation of the hair cells.

Bekesy (19) postulated his "law of contrast" to further limit the action of stimulation. It says that the nerve excitation is particularly great in a region of the basilar membrane that forms a boundary between relatively little movement and relatively great movement. The difference will be greatest in the region of a maximum, for there are two transitions: from weak to strong and from strong to weak; and the two contrast effects are added. Even in the face of heavy damping in the cochlea, pitch perception has specificity, because this narrowing of response is superimposed upon that already afforded by the local eddy (19). Specificity, though lost at first, is finally regained.

In general, the traveling-wave theories have difficulty with the specific nature of the assumptions they make about how the stapes acts in initiating the cochlear waves and about the paths of travel these waves follow. For example, bone conduction can transmit vibratory energy to the cochlea from any of several directions, bypassing the stapes. In the case of otosclerosis, even though hearing is impaired to aerial sounds, it is not seriously affected (in simple cases) for vibrations communicated to the bones of the skull (111, 112). In addition, Wever, Lawrence, and Smith (204) have found that sounds applied to the round window are as effective in producing electrical potentials in the cochlea as when applied to the oval window. It is evident that there is no one specific, necessary path acoustic energy must travel to the cochlea; and it is this problem that the wave theories must deal with.

Finally, according to the traveling-wave theories, introducing two tones at opposite ends of the cochlea should produce a pair of waves traveling in opposite directions. Because the theory assumes heavy damping for high tones, the waves should expire without meeting. With lighter damping, as assumed for low tones, these waves should meet to form a standing wave pattern. Wever (199) placed measuring electrodes at opposite ends of the cochlea, then presented tones at both ends, either singly or together. The responses measured at the electrodes always differed, and for the high tones they differed as much as 18 dB (199). He concludes

that stimuli presented at both oval-window and apex pass freely and rapidly through the cochlear fluids and affect the basilar membrane in the same region and in the same fashion. The two stimuli together produce a pattern of action differing only in magnitude from that produced by one of them alone.

The later traveling-wave theories are alike enough that they may be regarded as alternative formulations of a common position. They attempt to account for the distribution of wave patterns over the basilar membrane as a function of frequency. All of them have been greatly influenced by Bekesy's empirical observations and follow his observations in the types and manner of variation of the wave patterns. The differences among the theories reflect their varying assumptions as to the essential variables and boundary conditions, and especially the simplifications that are found necessary in the mathematical treatment. The interested reader is referred to the following for further developments of traveling-wave theories: Ranke (146), Reboul (144), Zwislocki (213), Peterson and Bogert (142), Huggins (94), Fletcher (63), and Bergeijk (21).

FREQUENCY THEORIES

The second major division of classical theories of hearing is the frequency theories. They are subdivided into the "telephone" or non-analytic theories and the frequency-analytic theories. Rutherford (155) represents the former, while Meyer (123) exemplifies the latter.

Rinne (151) was the first to suggest a frequency theory. However, he did not develop a formal theory; he was chiefly concerned with the concepts of resonance and peripheral analysis. Essentially, he felt that peripheral analysis only creates a new problem, that of synthesis later on.

At the time, Voltolini (191) had the audacity to write that Helmholtz's theory was "the product of a great mind in an hour of weakness." He postulated a frequency theory, insisting that every hair cell responds to every sound, rather than some one cell to each discriminable sound. He argued that the larger the number of cells responding, the greater the acuity of hearing. He was the first to compare the ear with the telephone and the phonograph.

Rutherford's Theory

Rutherford's (155) theory assumes that the auditory nerve receives and transmits a pattern of stimulation that corresponds in all essential details to the pattern of the external sound. He postulates that all the hair cells can be stimulated by any sound, and, therefore, it is theoretically possible for a single hair cell to give rise to all the different auditory sensations. However, the larger the number of cells responding, the better the auditory acuity. According to the theory, analysis of a sound takes place at higher auditory centers.

Although Rutherford recognized the demands that his theory placed upon the auditory nerve fibers, he did not consider this factor to be a serious obstacle to his theory. In an attempt to determine the maximum rate of neural activity, Rutherford stimulated the nerve of a rabbit and found that the resulting electrical output pulses yielded an audible tone if run into a telephone receiver. However, he found impulses up to only 352 per second and was forced to turn to other observations which showed that the action current in the frog's sciatic nerve lasts only 0.0007 second; on this basis, he inferred that a frequency of about 1400 cps was possible. He believed that the true upper limits of frequency of the nerves had not been approached.

He criticized the concept of selective resonance, arguing that the transverse fibers of the basilar membrane are not isolated and free; and in some animals (rabbits and birds), there are two layers of fibers, sometimes with connective tissue binding the whole together. Also, he interpreted Hermann's evidence on "beat tones" as contrary to the resonance hypothesis (89). Hermann found that an external tuned resonator will not respond to a "beat tone" of two simultaneously presented tones. Rutherford argued that if an external resonator does not respond to a frequency difference, a resonator within the ear cannot be assumed to do so either.

Rutherford believed that the analysis of complex sounds was not a native capacity but a skill acquired through practice -- and one at which only a few persons achieve a high degree of proficiency. Rutherford assumed that the analysis of complex sounds is not a peripheral process but, rather, a central process.

Rutherford supported his assumption with existing evidence on cochlear destruction in animals. Baginsky (12) reported dogs lost hearing for high tones following destruction of the apex and the middle turn of the cochlea. However, if the basal turn of the cochlea had been destroyed, animals were able to hear both high and low tones after the operation. Contrary to Baginsky's results, Stepanow (169) reported that guinea pigs responded to low as well as to high tones after destructions in the apical region of the cochlea. Moos and Steinbrugge (127) reported humans had reduced upper limits of hearing as a consequence of atrophy of the nerve in the basal region of the cochlea.

Although this experimental and clinical evidence was considered to support the Helmholtz theory, Rutherford believed that it was not consistent or conclusive. He accepted the possibility of high-tone localization but found no evidence that the low tones were correspondingly restricted to the apical region.

Reformulation of Rutherford's Theory

Waller (193) and Ayers (10) presented variations of Rutherford's theory, and Boring (23) has reformulated it. For Boring, frequency of response in the auditory nerve is correlated directly with the frequency of sound waves. Greater amplitude of sound involves increased spread of excitation on the basilar membrane, and hence includes a greater number of nerve fibers in the conduction process. Once again, analysis of complex sounds is not a peripheral but a central affair.

The telephone theory explains binaural localization in terms of phase difference. In the telephone theory the tones are transmitted centrally at their proper frequencies and, consequently, in their incident phase relations; thus a phase difference can be appreciated directly. This matter of binaural phase localization provides an effective argument for the telephone theory as a valid explanation of auditory localization.

Perhaps the most salient criticism of all the frequency theories is their pre-occupation with pitch perception. However, this fault is probably attributable to the fact that they originated in opposition to resonance theories and seek to replace them.

In spite of the fact that individual auditory fibers cannot fire at a more rapid rate than 800 or so impulses per second, Wever and Bray (201) demonstrated that stimulus frequencies above the limit of individual fibers are reproduced faithfully by volleying in the auditory nerve as a whole -- at least up to about 4000 cps -- and thus provided new impetus for the frequency theories.

Frequency-Analytic Theories

The remaining type of frequency theory to be considered is frequency-analytic theory. This group postulates a special means apart from resonance for allocating different frequencies to different parts of the basilar membrane. Furthermore, this group accepts the principle of representing pitch by the frequency of nerve impulses.

Max Meyer's (123) theory is an example of a frequency-analytic theory, perhaps best known as the "leather-seat" theory of hearing. Meyer regarded the basilar membrane as leather-like in nature and as laxly suspended between the vestibular and tympanic scalae. The theory assumes that the inward movement of the stapes exerts a positive pressure on the cochlear fluid causing the response of the basilar membrane to be restricted to its most basal portion. When the bulge exceeds the elasticity of the membrane, it begins to spread to the more remote portions. The bulge extends in the apical direction only as far as necessary to provide room for the fluid displaced by the stapes.

Following the maximum extent of inward movement of the stapes, a reciprocal movement is initiated and causes a second displacement of fluid, but in a direction contrary to the first. As a result the membrane is drawn upward. This reversed motion of the membrane begins at the basal end of the cochlea and spreads toward the apex. The second movement of the basilar membrane can erase the original bulge and return the membrane to its initial position, if the backward movement of the stapes has the same amplitude and velocity as the preceding forward movement. If the reverse stapedial movement is somewhat less in amplitude, the second displacement of the membrane will erase the first only in the basal region, and the most apical part of the original bulge will remain undisturbed.

Meyer (123) conceived of the basilar membrane as nearly inelastic, subject to frictional resistance, and for all purposes completely dampened. Thus, the membrane does not transmit motion along its own length to any appreciable extent. Unlike the traveling-wave theories, Meyer postulated that the spreading is brought about through the fluid and not by any wave motion of the membrane as such.

Though Meyer was not definite, excitation of the hair cells probably occurs on the upward phase of every up-and-down cycle of displacement. Regardless, one excitation occurs for every cycle, and hence the nerve response has a frequency equal to the frequency of the stimulating sounds. Loudness is determined by the total number of hair cells stimulated.

Probably Meyer's theory has not received the attention that it deserves because of its difficulty. However, the theory treats the basilar membrane as a simple structure. Meyer's theory accounts for the masking of high tones in terms of overlapping: the low tones spread farther along the basilar membrane than the high tones do. In addition, the theory can account for combination tones as a feature of the action in the cochlea when two or more tones are presented at the same time. Finally, it cannot be argued that the theory is not ingenious in its conception of a mode of analysis without recourse to resonance.

The last theory of hearing to be reviewed is the volley theory (199). The volley theory is unique in that it combines the place principle and frequency principle, retaining the positive features of each and supplanting their deficiencies. Thus pitch is represented in terms of place on the basilar membrane -- and, hence, of particularity of nerve fibers -- and also in terms of composite impulse frequency. Frequency serves for the low tones, place for the high tones, and both represent the intermediate frequencies.

The auditory scale is divided into the low-, middle-, and high-tone regions, as the means of frequency representation are brought into play singly and in combination. The boundaries of these regions cannot be clearly delineated and must, therefore, be located only in a rough and tentative fashion. The evidence for this location indicates that frequency representation is accurately maintained from the lowermost end of the scale up to somewhere approaching 5000 cps, but not above (71); and specificity of nerve fibers (place of representation) occurs over a range from about 400 cps upward, but not below. Thus it appears that place joins frequency at around 400 cps and place takes over in the region of 5000 cps.

Loudness is represented as the change in the rate at which a given nerve fiber contributes to the total nerve discharge and also by the number of nerve fibers acting. It is suggested that any tone involves an extensive area of the basilar membrane, but that different portions of the area may be involved more or less. A certain central region is postulated as being most strongly stimulated, and other regions as stimulated less and less as one proceeds up and down the cochlea.

A major problem facing the traditional resonance theories was the scope of specific resonance. The volley theory attempts to limit the differentiation of cochlear elements for specific tuning to agree with the anatomical structure of the ear.

Since low tones are represented by the frequency of neural response, it is not necessary to assign specific spatial representation to them. Furthermore, it is postulated that some curtailment occurs at the upper end of the auditory range. Precise tuning need not continue all the way to the upper limit of hearing but may cease somewhat before this limit is reached. High-frequency stimulation would force responses in regions tuned to frequencies somewhat below, with a resultant decrement in sensitivity and pitch discrimination.

Evidence Supporting Wever's Place and Volley Principles

Because the experimental evidence which supports the volley theory is so large, only a brief review of the literature will be presented. Crowe, Guild, and Polvogt (34) found a relationship between a loss of acuity for high tones and the atrophy of nerve fibers and of the organ of Corti in the basal part of the cochlea in humans. Wittmaack (207), using a conditioned response technique in conjunction with experimental injury, reported that dogs responded to all tones from 50 to 30,000 cps before surgical operation. Then one cochlea was totally destroyed, and the other was damaged in all but the basal part. The animal responded to high tones, and histological examination verified that only a fragment of normal organ of Corti and nerve remained in the basal region.

Hughson, Crowe, and Howe (95) were the first to use the electrical responses of the cochlea to determine the effects of local injury. They found that, in cats, damage to the basal region caused a general reduction in responses, with the most serious effect upon the high tones.

Walze and Bardley (194), using cats, reported that basal lesions caused high-tone losses, and those in the apex of the cochlea caused losses of lower frequencies. However, lesions in the apex gave no noticeable impairments when they were small, and then when they were enlarged they caused rather general losses. The most apical lesion yielding restricted losses was 15mm from the basal end and it had its maximum effect upon a tone of 256 cps. Tones as high as 724 cps were also affected, but to a lesser extent. In general, the smaller lesions had effects over one or two octaves, and somewhat larger ones had far wider effects.

Smith and Wever (166) measured the electrical response of the guinea pig cochlea following stimulation with a tone of 1000 dynes per sq. cm., maintained for four minutes. They found that when the stimulating frequency is low the losses are about the same throughout the auditory scale or, if anything, are more serious in the middle and upper regions of the scale. But if the frequency is high, the low tones are progressively less affected.

When the stimulation is moderate, the potential losses are only 10 or 15 dB, and there is no apparent anatomical change: the cochlea appears histologically normal. Wever argues that the stimulation possibly causes two kinds of alteration in the sense organ. One, of a milder sort, is an impairment of the capacity of the cells to generate electrical potentials. This is not a permanent impairment because there is a slow recovery over a period of hours or days, depending on the severity of the stimulation. The other alteration is obvious mechanical damage, and from it, little or no recovery can be expected.

Smith and Wever (166) concluded that, for low tones, the spread of action is very great when the stimuli are strong. The spread must be considerable, even for the high tones, because sensitivity to these tones is impaired after overstimulation by other high tones, as well as by the low tones.

These studies all point to fairly specific cochlear localization for high tones. It is to be remembered that a loss of hearing for only the low tones is rare. When acuity is impaired for the low tones, it is impaired for the middle tones, and usually the high tones as well. Often, when the curve of hearing is depressed at the low-frequency end, it continues to fall, either gradually or precipitously, as the high frequencies are approached. Furthermore, whereas basal atrophies are common, local atrophies elsewhere in the cochlea are extremely rare (85). Thus low-tone hearing cannot be studied in a way that is strictly comparable to some of the studies just described for high tones. It is apparent here, apart from any special consideration of volley theory, that there is some important, even fundamental, difference in the ear's behavior toward the high and low frequencies.

Finally, Stevens and Davis (172) reported an experimental confirmation of the volley principle. They measured action potentials in cats' auditory nerves when maximal stimulation was given over a wide range of stimulus frequencies. There was a sharp reduction in size of response at two critical frequencies: 850 cps and 1700 cps. At low frequencies all fibers can follow the stimulus, discharging with every cycle of pressure change. When the frequency is around 850 cps, the discharge amplitude drops to about half its former value, presumably because of the absolute refractory period of the auditory nerve fibers. At this stage, volleying begins. When twice the frequency is reached, at 1700 cps, there is a further abrupt drop to one-half the previous amplitude of response, and three "platoons" now share the burden. Above 3000 cps, the response becomes asynchronous and random. The following literature gives further relevant information about the volley theory: Larsell, McGrady, and Larsell (108); Larsell, McGrady, and Zimmermann (201); McGrady, Wever, and Bray (118, 119); Culler (35); Culler, Coakley, Lowy, and Gross (36); Wever (199); and Wever and Lawerence (203).

A major drawback to the volley theory becomes evident when electrical activity is recorded at central auditory centers. Kemp, Coppee, and Robinson (102) inserted electrodes at various levels of the auditory pathway and recorded action potentials produced by sound stimulation. The upper limit of synchronization for second-order neurons was found to be about 2500 cps, whereas that for third-order neurons was only about 1000 cycles. Davis (37), using anesthetized animals, was unable to demonstrate any synchronized response to pure tones in the auditory cortex, although a succession of clicks was reproduced to about 100 per second. These studies clearly indicate progressive reduction in synchronization of activity between receptor and cortex.

CONCLUDING REMARKS ON THE CLASSICAL THEORIES

In concluding this section about the history of theories of hearing, it is essential to point out that the four major theories -- resonance, telephone, traveling-wave, and standing-wave theories -- really constitute stages in a continuum, and fundamentally their similarities outweigh their differences. It is possible to obtain patterns of response corresponding to the predictions of any one of these types of theory by manipulating only two conditions, the absolute stiffness and the rate of variation of stiffness along the basilar membrane. Bekesy (19) demonstrated these transitions from one form of response to another in some of his mechanical models.

This consideration points out the need for further information about physical conditions within the cochlea for more precise measurements of the variables that govern responses to sounds. Finally, a theory of hearing must be developed to account for all the phenomena of hearing. Most theories of the past have been preoccupied with explaining pitch perception. Important though this feature of auditory experience may be, it is only one of a vast array of experimental phenomena, every one of which has to be accounted for before a theory can achieve its sophisticated and final form.

PERIPHERAL CODING OF AUDITORY INFORMATION

It is known that the human auditory nerve is composed of myelinated nerve fibers of moderate and quite uniform size (three to five microns in diameter). The cell bodies lie peripherally in the spiral ganglion inside the cochlea. They are bipolar cells, and synaptic connections are absent in this ganglion. Man has between 25,000 and 30,000 afferent fibers in each ear, as determined by ganglion cell counts. These figures are about equal to the number of sensory cells (hair cells), and both are distributed uniformly throughout the length of the basilar membrane in the cochlea (38, 40, 173).

The peripheral endings of the sensory nerve fibers are nonmedullated throughout the organ of Corti. They are completely naked and are regarded as a dendritic system. Thus all-or-none impulses followed by refractory periods cannot be assumed until the auditory fibers acquire their myelin sheaths in the habenula perforata.

However, Tasaki (178) has found all-or-none impulses in the auditory nerve at the internal auditory meatus, with a latency of one millisecond or longer. This form of conduction imposes a severe limitation for the coding of incoming auditory information.

Presently, the major problem confronting auditory theory has been determining how the frequency and the intensity of an auditory stimulus are coded into all-or-none impulses, separated by silent intervals and traveling in a large number of parallel, insulated channels. Secondly, the coding of information for auditory localization has also been an important problem for many years.

Bekesy has shown that the cochlea acts as a mechanical acoustical analyzer, and that the position of maximum mechanical activity along the basilar membrane is a function of frequency (20, 39). Thus frequency, particularly of high tones, is coded by certain channels (nerve fibers) along certain parts of the basilar membrane. This is the familiar place principle.

Furthermore, it is known that for low frequencies (below 2000 cps or thereabouts) nerve impulses in the auditory nerve tend to group into volleys because each sound wave acts as a separate stimulus (18, 20). This is the frequency or volley principle of auditory coding.

Frequency of discharge forms the basis for coding the information concerning the intensity of the stimulus in some sensory systems. However, it has been shown that frequency of discharge in a given auditory fiber is a function of intensity only within a very limited dynamic range: not more than 20 or 25 dB (71, 100).

It is more likely that the intensity of an acoustic stimulus is represented by the total number of fibers that fire in a unit time, rather than by the total number of nerve impulses in a given length of time.

The binaural difference in intensity and the binaural difference in arrival time for corresponding sound waves are important determinants of auditory localization. The precedence effect is highly significant even when the difference is only a fraction of a millisecond. The separation of the two ears and the intervening acoustic baffle of the head provides a built-in neural code -- based on differences in time and in intensity, and appropriate to low and to high frequencies, respectively -- to carry information about the direction an incoming sound came from.

More obscure is the possibility of certain small-scale time differences (differences in latency) among the responses of the nerve fibers of an individual ear. Traveling waves on the cochlear partition impose certain necessary differences in times the crests of the waves arrive at different points along the cochlea. These time differences depend on the frequency of the sound wave in question (180). Thus the consequent systematic differences in the times impulses arrive in different nerve fibers can be of some use -- although for what purpose is still unknown.

Katsuki, Sumi, Uchiyama, and Watanabe (100) have shown that individual elements in the midbrain and the cortex are more "sharply tuned" than the neurons of the auditory nerve. It is evident that inhibitory processes are operating, except in a given channel or set of channels, thus providing selective tuning for a given frequency of an auditory stimulus (68). It is assumed that differences in intensity of stimulation at different points along the cochlear partition somehow cause the suppression. However, the intensity differences do not seem large enough to account for the sharpness and precision of frequency discrimination (41). It is possible that systematic differences in time of arrival, as a result of the delay in the traveling wave, could enter into this particular code to sharpen frequency discrimination. However, impulses that arrive later from more apical regions would produce excitatory effects in the tuned units at higher levels; and on the other hand, the impulses from the more basal region that the traveling wave traversed earlier would not excite these particular units, but would somehow be suppressed (41).

It has been suggested that the earlier synchronized impulses in each volley, from the more basal regions, are not merely suppressed but carry information about the time the individual low-frequency sound wave or burst of high-frequency sound arrived. This serves as a cue to lateralization and may be the primary function of all well-synchronized neural volleys.

Differences in Coding for Low and High Frequencies

There may be, within the cochlea, differences between low-frequency detection and coding and high-frequency detection and coding. The two overlap in a large middle-frequency range from 500 cps (or lower) to perhaps 2000 or 3000 cps. The frequency principle differentiates between high and low tones; it can only operate in the low-frequency range. Even though this part of the auditory system is the direct extension of the sense of vibration, intensity discrimination is not sacrificed for an extended dynamic range. Stimulation is still substantially wave by wave, and the refractory period restricts the range of frequencies that can be transmitted directly.

The mechanical frequency analyzer of the cochlea can detect and discriminate frequencies above 2000 cps, well beyond the effective range of the turtle and some birds such as the pigeon (205). Thus the mechanical frequency analyzer was a biological breakthrough, yielding the place principle as the primary coding mechanism for high tones (4000 cps and higher).

Davis, Fernandez, and McAuliffe (45) have found summation of excitatory effects for successive high-frequency stimulation. The DC summating potential mechanism of the inner hair cells, a second mechanical detector system, detects the envelope of the stimulation pattern directly before neurological coding has taken place (42). The summating potential is large in the basal turn and seems important for the detection of high-frequency signals.

The mechanical frequency analyzer, an extension of the sense of vibration, serves as the coding mechanism for middle and low frequencies. In addition, the frequency analyzer and the envelope detector have evolved as two entirely new mechanical analyzing devices. These peripheral analyzers provide greater variety and latitude in peripheral neural coding. The new channels and codes of the auditory system do not replace but are added to more primitive systems. As a result the psychoacoustics of low-frequency sounds will probably be different from and more complicated than the psychoacoustics of high-frequency sounds.

Thus we might conclude that the peripheral mechanism for coding pitch and other auditory information is much more complex than Helmholtz had originally thought. Impulses in the auditory nerve provide information in three ways: by the channels in which they travel, by their number, and by the time relations among them. The volley principle provides information about pitch perception, but the time differences between volleys from the two ears contribute to auditory localization, and possibly time differences between different fibers in the same ear assist in the operation of the place principle for the perception of pitch.

Simple Auditory Systems

In reviewing experimental results of how birds and fish behave toward tones, we find a contradiction to the conclusion above. In the first place, neither the range of heard frequencies nor the ability to discriminate between them can be related in any simple way to the degree of development of the peripheral auditory apparatus. In particular, a cochlea need not have developed to the mammalian degree of complexity. Fish have no basilar membrane (in fact, they have no cochlea at all). The organ of Corti in birds lacks the arches of Corti and certain other of the mammalian refinements (8, 150). Furthermore, the auditory tracts and nuclei of these lower forms appear to compare favorably in size and organization with the system in cat or man (98). The bird, for example, is deficient in certain structures thought necessary for refined discrimination between tones. There appears to be no differentiation between internal and external hair cells, and birds have no well-defined auditory cortex. If we assume that the neural mechanism determining tone reception is similar throughout the phyletic scale, then the fact that the fish, with its primitive auditory neurology and without any basilar membrane at all, may exhibit better pitch discrimination than some people argues strongly for the viewpoint that both the requisite neural equipment and the interactions that go on within it are relatively simple and uncomplicated.

A Dilemma

Thus a dilemma exists, since the pressing questions today are the same ones that have always faced students of hearing: first, what is the system of neural connections in the cochlea; and second, what actions are produced in and what interactions occur among these neurons as the cochlea converts mechanical motion into nerve impulses and the consequent perception of pitch? It is hoped that continued research will ultimately answer these persistent questions and resolve the dilemma of how much neural equipment and what processes are necessary for pitch perception.

PART II: AUDITORY PHENOMENA

INTRODUCTION

This section will review some of the experimental findings related to pitch perception. We will examine the auditory phenomena that are experienced by the auditory behavior of both man and animals. Our primary interest will be the role of frequency in determining auditory experience. The reader should keep in mind that pitch is just one of three psychological variables that a truly adequate theory of hearing must account for, and it is hoped that the reader will gain an appreciation of the difficulty of constructing an adequate theory of auditory phenomena from the discussion that follows.

Frequency Sensitivity of the Ear

The ear's sensitivity to different frequencies has been investigated extensively with a variety of techniques and procedures (165). The majority of the studies report that the ear is most sensitive to the middle frequencies (about 2000 cps to 4000 cps), and that sensitivity decreases rapidly as the extremes of the frequency continuum are approached (64).

Wever and Bray (201) attempted to determine the lowest frequency at which tonal recognition is possible. They found that all observers reported tonal character at 25 cps with intensities above 15-20 dB. The extent of tonal recognition varies inversely with intensity of the tonal stimulus. Other investigators have placed the lower limit for tone at 18 cps (25). Bekesy (19) has demonstrated that pitch discrimination is present all the way down to one cps. The difficulty in accurately determining the lower limit of tonal recognition stems from the fact that the transmission system of the middle ear and cochlea responds to even pure sinusoidal waves with a complex spectrum of vibrations.

It is interesting to note that the threshold values obtained for minimum audible pressures, measured at the eardrum, are from 10 to 20 dB above the values for minimum audible fields. Thus when a subject is listening to a tone which he is just able to hear, the intensity of the sound field outside his ear is less than the intensity at his eardrum.

A number of aspects of the ear's sensitivity -- such factors as the threshold of feeling, tonal lacunae, audiometry and developmental factors affecting sensitivity -- will not be discussed in the present paper. However, the ear's sensitivity to electrical stimulation will be treated later in this paper.

Differential Sensitivity for Frequency

The size of the differential limen for pitch has always been of special interest, since it defines the minimal differentiation in the inner ear that a place theory of pitch, like Helmholtz's, must have. The early determination of the difference limen (DL) for pitch stems from the work of Preyer, Luft, and Meyer in the latter part of the 19th century. Results of their experiments, using such apparatus as stretched strings and hand-struck tuning forks, yielded exceptionally small values for the DL. Vance (190) gives an historical summary of the problem.

Shower and Biddulph (163), using the thermionic technique, performed a definitive study of the difference limens. They obtained limens so large that the number of discriminable pitches, even at the intensity which gave the maximum, was only about 1500. Furthermore, they found that below 500 cycles "delta f" (the just noticeable increment in frequency) is approximately constant with frequency until the extremely low frequencies are reached. Shower and Biddulph reported that frequency sensitivity varies with sensation level: delta f/f becomes smaller, or more sensitive, as the sensation level is increased. Finally, the results of the study show that bone conduction and binaural presentation correspond fairly consistently to and lie definitely below the obtained monaural air conduction curves.

Thus it seems that improved techniques and better experimental control reduce the number of discriminable pitches. It may be asked why poor control helps an individual make more accurate discriminations. Perhaps factors other than the fundamental frequency of the stimulus affect the size of the difference limen.

It is known that practice reduces the limen and that individual differences make the limen vary. Psychophysically, the method of limits and the method of right-and-wrong cases do not yield comparable difference limens. The method of limits, as Luft used it, measured the average spread of the equal category. The method of right-and-wrong cases, as Meyer and Vance used it, eliminated the equal category. Luft's limens therefore depend partly on the S's attitude about the meaning of the categories of judgment; Meyer and Vance's are partly dependent on the variability of the organism's adjustment to the stimulus (190). Finally, the limens of continuous change are larger than the limens for abrupt change. It is easier to perceive a difference when the impressions are separated by a "contour" than when the one fades slowly, spatially or temporally, into the other.

ABSOLUTE PITCH

Absolute pitch is the ability to name a tone that has just been heard without comparing its pitch to that of a standard. Perhaps the reader knows of a person who can recognize and name precisely the pitch of a musical note without the aid of a standard reference. Many cases of absolute pitch have been recorded in the literature, but Stumpf's discussion of Mozart's sense of pitch marked the beginning of psychological interest in the problem. Ideally, we would like absolute pitch to mean the ability to name the pitch (or frequency) of a pure tone without the aid of such devices as whistling or humming the note.

Many investigations have shown that absolute pitch can be improved as a result of practice (13, 81, 143, 196). Gough (81) who trained 90 college students on the piano, has shown that the subjects improved from an average error of 5.5 semitones on the first trial to 4.5 semitones on the last trial. The individual practice curves were extremely irregular from subject to subject and gave no evidence of a plateau at any point. All the curves showed that average error per trial decreased as a result of practice. The fewest errors were made in the middle octave, and the distribution of errors increased toward either end of the scale, except that the highest note and the lowest note had the fewest errors of all.

Mull (129) has shown that practice definitely improves the ability to estimate pitch in an "absolute" manner. Although she trained two groups of subjects, the more pertinent facts were obtained from the group that practiced identifying the pitch of middle C. This group gave judgments that were correct 40 percent of the time before training; but after training, their judgments were correct 82 percent of the time. When the same group learned to select middle C from a scale consisting of nine tones, one separated from the next by only eight cps, their final performance was an average error of 29 cents (100 cents = 1 semitone). Furthermore, decreasing the distance between tones in the scale did not change the size of the average error appreciably.

Wedell (196) attempted to determine whether untrained persons can learn absolute pitch. An oscillator was used to generate pure tones. The results showed that relatively "unmusical" observers can increase their accuracy in assigning pitch numbers to pure tones. He found that the greatest increase in ability occurred during the first few practice sessions. In addition, the course of the learning was very irregular, and there were large individual differences.

Contrary to the studies reported previously, Wedell found that average error was greatest in identifying tones from the middle of the scale, with errors gradually decreasing toward the ends of the scale.

Bachem (11) studied 90 cases of "genuine absolute pitch," seven of which possessed infallible absolute pitch over the whole scale of the piano and for all musical instruments and physical apparatus with which they were tested. These people based their decision upon the immediate perception of tone-chroma, and seemingly relied on recognizing the "height" of the tone to identify the particular octave that the tone belonged to.

Psychology of Music

Since practice can improve pitch perception, questions may be raised about the value of experimental techniques for learning music. Since music is conveyed by sound waves, recording and analyzing those sound waves should provide an objective medium for analyzing musical performance.

Seashore (158) states that all musical performance may be expressed in terms of four media -- the tonal, the dynamic, the temporal, and the qualitative -- which correspond to pitch, intensity, duration, and timbre, and are measurable respectively in frequency, amplitude, duration, and form of sound waves. Seashore believes that the medium of musical art lies primarily in artistic deviation from the fixed and regular, such as rigid pitch, uniform intensity, or pure tone. According to Seashore (158), then, performance may be expressed quantitatively by measuring the deviations in each of the four groups of attributes. Although Seashore goes on to present a method for learning musical performance, it is interesting that his method draws heavily on findings from investigations of auditory phenomena.

Pitch of Complex Sounds

Pitch is mostly defined in reference to the perception of pure tones. However, it is evident that noises and other aperiodic sounds may have a more or less definite pitch. The dominant components of a complex sound usually determine the perceived pitch. Ekdahl and Boring (56) asked observers to judge the pitch of a tonal mass composed of numerous frequencies, all lying within a restricted band. The observers named a pitch which was close to the center of the band. However, the pitch of a noise or a tonal mass is more or less indeterminate, depending upon the range of frequencies present.

When there are few enough components in a sound, the ear can resolve the complex into its individual frequencies, a phenomenon which is termed Ohm's acoustic law. Some investigators (172, 175) believe this capacity depends upon an ability to discriminate the separate areas of excitation on the basilar membrane.

Aural Harmonics

The problem of aural harmonics may be related to perceiving the pitch of complex tones. Briefly, when the ear responds to a loud pure tone, it distorts the impinging stimulus by introducing harmonics, which are overtones of the fundamental frequency. Wegel and Lane (197) were able to measure the magnitude of the aural harmonics and established that their frequencies are exact multiples of the tones producing them. Furthermore, the strength of the harmonics depended

on both the fundamental frequency of the inducing tone and its intensity. (See Wever and Bray (202) for a more direct method -- cochlear microphonic -- of studying aural harmonics, and Wever (199) for a more detailed discussion of distortion in the ear.)

RELATION OF PITCH TO STIMULUS DURATION

What happens to the pitch of a sound when its duration is reduced to smaller and smaller values? Also, how many cycles are required for a tone to be perceived as having a definite tonal quality?

Burck, Kotowski, and Lichte (28) found that the absolute time necessary for identifying the pitch of a tone is shortest in the middle range of frequencies, where it is approximately 0.01 second. They also found that from three to four waves are required to specify the pitch of tones below 200 cycles. At 1000 cycles about 12 waves are needed, and at 10,000 cycles the number jumps to about 250.

Perhaps the most sensitive measure of whether or not a tone has pitch is the precision with which the pitch can be identified. Since the DL is the measure of precision in sensation, we might inquire about how duration affects the DL for frequency discrimination. Using this measure, Bekesy (19) found that pitch was lost gradually as the duration of the tone was shortened.

Other experiments have determined how much the onsets of two tones must be separated in time to appear successive rather than simultaneous (177). Interestingly enough, the times involved are rather similar to the time required for recognizing the pitch of a tone. The importance of such findings to telephone communication is obvious.

Auditory Fatigue

Conversely one might ask whether the ear's responsiveness is reduced seriously after prolonged stimulation. Rosenblith has shown that steady stimulation reduces the apparent loudness of a tone and raises the intensive threshold for immediately subsequent stimulation.

Since the two cochleae presumably do not have separate cortical projection areas -- and because the physical stimulus does not confine itself to one cochlea -- the site of auditory fatigue, whether central or peripheral, still remains to be determined. Wever (199) gives a more detailed discussion of this problem.

Weinberg and Allen (198), measuring the frequency with which a tone must be interrupted to give a just-continuous sensation, found that the usual interruption frequency was lowered after two minutes' stimulation by a tone of that pitch. They found that this adaptation was confined to a small band of frequencies and therefore interpreted their results as supporting a place theory of audition.

Bekesy (19), who used a binaural procedure, has reported that exposure to a given tone causes a temporary reduction of sensitivity to tones over a broad range of frequencies on either side of the fatiguing tone. The difference between Bekesy's study and Weinberg and Allen's, is that the latter stimulated only one ear.

Pearce (139) has found that, if the ear is stimulated for 45 seconds with relatively pure tones, presumably of comparable intensity, subsequent tones between 256 and 3000 cycles may appear less loud than previously. He has also found that the tone's loudness decreases more if the continued tone is the same pitch rather than a different one. Also, there is more adaptation after prolonged stimulation by lower-pitched tones than with higher-pitched tones.

Pearce's results imply that the amount of adaptation depends on the frequencies. Assuming that the adaptation is localized in the vibrating masses of the cochlea, results from stimulating with lower-pitched tones are in better accord with a frequency explanation of pitch perception, and those from stimulating with higher tones fit with a place explanation better.

At any rate, further research is needed to work out a precise set of functional dependencies relating the extent of auditory fatigue to various stimulus durations, intensities, and frequencies.

Frequency-Intensity Relationship for Pure Tones

Perhaps the first person to notice the change in pitch as a function of intensity was Wilhelm Weber in 1828, while listening to the sound of a tuning fork as it died away in strength.

A great deal of investigation has gone into this problem, and the majority of the studies indicate that, for low tones, the pitch decreases with intensity; and for high tones, the pitch increases with intensity. For certain tones in the middle range (e.g., 2000 cps), there is no change in pitch (60, 113, 126, 167, 170, 183, 199, 212).

The frequency-intensity relationship presents a number of problems to auditory theories. It challenges a frequency theory that attributes pitch to nerve-discharge rates, since shifts in pitch can result from changes in intensity. Place theories are not immune to the frequency-intensity problem, either. Fletcher (60) has attempted to explain the problem in terms of a place theory, in which the pitch change is mediated by a shift in the position of maximal stimulation on the basilar membrane. Fletcher assumes that the portions of the ear which respond maximally to low frequencies act in a manner similar to stretched strings, whose resonant frequencies increase with increased intensity, and that the portions which respond maximally to high frequencies act in a manner similar to pendulums and tuning forks, whose resonant frequencies decrease with increased intensity. But what about the middle range of frequencies? Unfortunately, it is not explained whether they are strings, or forks, or neither.

Stevens (170) has attempted an explanation in terms of the resonant characteristics of the ear, but without reference to particular types of resonators. He assumes that, with increasing intensity, the portion of basilar membrane at the position of maximal stimulation becomes overloaded; the excitation on either side then grows at a faster rate. It is interesting to note that Stevens implies spread of action in the cochlea, which is not often admitted in a place theory. At the same time the disturbance undergoes a skewing process imposed by the overall properties of the ear, so that there is only one maximum. Thus for the high tones, there is a shift toward the basal end, with a rise in the pitch; for the low tones, the shift is toward the apical end, with a lowering of the pitch. Since the frequency region where pitch remains stable is where the ear is most sensitive, the middle tones lie at the center of the basilar membrane and do not shift their positions with intensity. The position shifts are attributed to contractions of the middle ear muscles and overloading of the basilar membrane.

Thurlow (183) reports that the pitch of a tone presented to one ear can be changed by introducing a tone of the same frequency in the other ear, provided both tones have fairly high intensity. While the effect is most prominent if the second tone has the same frequency as the first, this is not a necessary condition. It is evident that the pitch change which occurs through binaural interaction casts grave doubts upon the hypothesis of the mediation of pitch by the position of maximal stimulation. Furthermore, Snow (167), investigating how low tones change pitch as a function of intensity, found that some of his subjects showed changes, but others did not. Those who did, varied greatly among themselves in the amounts of change, and even a single subject varied from day to day. It is obvious that the intensity-pitch effect has none of the regularity it should have if it depended on some simple peripheral process.

Wever (199) believes that the qualitative change in pitch that a change of intensity brings about might be a perceptual illusion. In the volley theory the stimulus variables of frequency and intensity both have cochlear actions that involve the dimensions of time and space, though in different ways. One possible basis for the intensity-pitch illusion would be that these ways are not separate, but merge in minor respects. See Wever (199) for a further elaboration of his explanation.

It cannot be denied that the pitch shift is relatively small, but the fact remains that it is definite and measurable; and any theory of hearing that pretends to be complete must explain it adequately.

Frequency-Intensity Relationship for Complex Tones

Fortunately for music lovers and musicians, the complex tones produced by most musical instruments suffer only very slight changes of pitch with intensity. Lewis and Cowan (113) have found that when four skilled musicians played a certain interval on a violin, first very softly and then very loudly, the relation between the objective frequencies constituting the interval was not significantly different in the two cases. Since the players were judging the intervals in terms of subjective pitch, Lewis and Cowan concluded that the pitch was not changed by intensity.

Fletcher (59) has shown that the pitch change as a function of intensity is about five times as great for a pure tone (200 cps) as for a five-partial tone (fundamental frequency of 200 cps). Possibly the complex tones contain the frequencies whose pitch changes vary slightly with intensity. It is possible that these partials determine the magnitude of the apparent change of pitch when the complex tone is varied. Or, possibly, once complex patterns of stimulation are initiated in the central nervous system, they are not easily altered by energy changes.

Subjective Scale for Pitch

The crossroad of physiological and psychological research in hearing is psychophysiological acoustics. Its function is to determine the physiological mechanism underlying the psychological sensations of hearing. If both the psychological and the physiological phenomena of hearing turn out to be similar functions of the physical dimensions of the stimulus, it is assumed that the physiological function determines the psychological function. Constructing a subjective scale of pitch represents such an approach.

Stevens and Volkmann (175) have obtained a pitch scale by assigning numerals to tones in such a way that the numerals have some definite relation to the pitch of the tones. Stevens, Volkmann, and Newman (176) had also presented a previous pitch scale. The two studies differ only in the type of apparatus and method used.

Stevens and Volkmann (175) used the methods of equal sense-distances and fractionation to construct their pitch scale, which differs from both the musical and the frequency scale, neither of which is subjective. The unit of the scale was called a mel, which was one thousandth of the pitch of a 1000 cps tone. The close agreement of the pitch scale with an integration of the differential thresholds, using Shower and Biddulph's data, indicated that, unlike the DL's for loudness, all DL's for pitch are of uniform subjective magnitude.

Since there was close agreement between the difference limens and the obtained pitch function, it was concluded that, at a constant loudness level, all the DL's for pitch are of equal subjective magnitude. They also concluded that all the just noticeable differences (JND's) for pitch were essentially equal in subjective size. On the other hand, the DL's for intensity varied, so it was concluded that the JND's for loudness are not subjectively equal.

The obtained pitch function was then related to the experimentally located positions of vibration on the basilar membrane. There was a close correspondence between the locations of the resonant regions of the basilar membrane, the integrated DL's of Shower and Biddulph, and the pitch function.

Stevens and Volkmann concluded that we detect the difference in pitch of tones by a change in the locus of excitation on the basilar membrane and discriminate intensities by adding excitation to the excitation already present on the basilar membrane.

Implicit in such a conclusion, is the acceptance of Helmholtz's conception that the basilar membrane is tuned so that different portions resonate to different frequencies, and that pitch perception is perceiving the location of the resonating area.

MASKING

There are two conditions under which a normal person will fail to respond to an above-threshold stimulus. One condition is auditory fatigue, and the other is masking. Briefly, masking is an increased threshold for one sound because another sound is presented simultaneously. Binaural masking exists as a separate phenomenon, but it is negligible in amount in comparison with monaural masking. Of special interest is the fact that masking is greater in the high-frequency direction than in the low-frequency direction (197). This is obviously due to aural harmonics, each of which may serve as a masking influence if sufficiently intense.

Many investigations have demonstrated the existence of masking, but the locus of masking, whether peripheral or central, remains to be determined (19, 61, 62). Wever (199) indicates that masking occurs in the nerve action beyond the cochlea. (See reference 199 for a more detailed discussion.)

HEARING BY ELECTRICAL STIMULATION

All of the experiments reported previously were based upon vibratory (mechanical) stimulation of the ear. Since the ear behaves like a condenser microphone, it is interesting to know how electrical stimulation affects pitch perception. The electrophonic response occurs when an alternating current passes through the head, resulting in an auditory sensation. This phenomenon has been studied by a number of investigators (9, 75, 76, 101, 171).

Gersuni and Volokhov (75) report that observers can hear a tone when stimulated by a sinusoidal wave as low as 17 cycles. Stevens (171) found his subjects did not hear tones below 125 cycles and concluded that this was the lower threshold limit for electrical stimulation by purely sinusoidal currents, without shock. In any case, both the lower limit and the high-frequency limit for auditory sensation are restricted by an intensity increase of about 20 dB above threshold. Such an increase in intensity causes a combined burning, tickling, and pricking sensation. The tones produced by electrical stimulation lack the purity of tones heard in the usual way. In addition, the electrophonic phenomenon injects considerable distortion.

A "frequency theory" would most likely argue that the electric current stimulates the auditory nerve directly. However, such an explanation implies that there is a brain structure with the properties of either electrical or mechanical resonant systems. Stevens (171) states that the basilar membrane, loaded as it is with the hair cells of the organ of Corti which produce an electrical potential whenever they are disturbed, should bear a sufficient net charge to be able to respond mechanically to an alternating electric current. Since the basilar membrane is already tuned mechanically, Stevens argues that the alternating potential would create vibrations only in that portion of the membrane which is tuned to the frequency of the alternating current. However, Stevens fails to explain how the net charge on the hair cells arises.

SUMMARY AND REVIEW

We have reviewed the auditory phenomena which are most clearly related to pitch perception. It is evident that the explanation of these and other auditory experiences (consonance and dissonance, combination tones and beats, loudness, timbre, etc.), not discussed in the present paper, is one of the main tasks of auditory theory. From our review of the history of pitch perception, we can discriminate two main principles that have directed the explanation of auditory phenomena: the place principle and the frequency principle have served as guide posts and, perhaps, blinders for auditory theories. Despite the validity of both principles, one alone is not sufficient to explain all of man's auditory experiences.

Historically, various men have developed explanations of auditory phenomena based on one principle or the other and, in some instances, a combination of both principles. The questions that have plagued the field of audition still remain unanswered today. Namely, how specific is the response of the ear to tonal stimulation? Some people have argued for complete specificity; others dismiss the question as futile. Even Helmholtz admitted a certain degree of spread of action on the basilar membrane. Secondly, how effective is the frequency principle in representing the physical parameters of the auditory stimulus? These and many other questions still remain to be completely answered and, despite the abundance of accumulated knowledge, how the ear responds to tonal stimulation remains an unsolved mystery.

The last section of this paper will present the results of physiological and anatomical studies of the auditory system, to illustrate the validity of the frequency principle and the place principle. In addition, it will discuss recent developments, as well as the future directions of auditory research which hopefully will lead to an adequate explanation of pitch perception.

PART III: PHYSIOLOGY AND ANATOMY OF THE AUDITORY SYSTEM

INTRODUCTION

It appears that studies of the physiology and the anatomy of hearing have concentrated rather heavily on the cochlear end organ. Next most numerous have been studies of the cortical auditory areas. In comparison, the central pathway between the acoustic nerve and the cortical termination has received only sporadic consideration.

This section of the paper will review the physiological and anatomical findings about the auditory system, and point out whatever significance they may have for the "place" and/or "volley" principle. First, we will briefly consider studies of the cochlea and auditory nerve, then studies of the auditory pathway and the auditory cortex.

LOCUS OF RESPONSE IN THE COCHLEA

There are many ways to determine the place on the basilar membrane that a particular frequency stimulates. Many investigators (35, 36, 174) have used such techniques as stimulation deafness, depressant drugs, and mechanical lesions to determine the site of stimulation on the basilar membrane. Most results show that the low tones are located at the apex of the cochlea, and the high tones are located at the basal end.

Stevens, Davis, and Lurie (174) found that the low tones are crowded together at the apical end of the cochlea, and they argue that this explains the difficulty in proving specific resonance to low tones, as well as the ear's poorer relative differential sensitivity at low frequencies. Furthermore, since the external hairs are highly innervated as compared to the simple innervation of the internal hair cells, tones are differentiated more poorly when the stimulus is so weak that the external cells alone are activated. Pitch perception is best when the internal hair cells are stimulated by a more intense stimulus.

The majority of studies indicate that a single tone produces a great spread of activity along the basilar membrane. Thus it appears necessary to invoke some device like the principle of maximal stimulation or Bekesy's contrast effect, if a place principle is to explain pitch perception and the ear's remarkable sensitivity to small frequency differences. See Horton (92), Wilkinson and Gray (206), and Wever (199, 200) for further detail.

STIMULATION-DEAFNESS STUDIES

Various theories of audition can be tested by exposing animals to intense tones for long periods of time and then seeking functional and anatomical evidence of specific damage to the auditory mechanism (43, 44, 117). Two types of damage result from prolonged intense tonal stimulation. One is gross damage, such as intra-cochlear hemorrhage or rupture of Reissner's membrane, and the other is degeneration of the external hair cells. Generally, the loss of sensitivity is greatest in the frequency range between 700 and 1700 cps, although the exposure tone is usually of a higher frequency (about 2500 cps). Horton (93), for example, found that impaired sensitivity extended to tones other than the exposure tone. These studies appear to uphold a place theory of pitch perception, as opposed to a frequency theory, but we are forced to think of a "zone" rather than a "place" of reception. Although most of the reported studies have used guinea pigs as subjects, there is an astounding similarity between the sensory mechanisms in man and in this animal. The fact that the guinea pig's cochlea has four and one-half turns, instead of the two and one-half turns in man's, appears to be of no consequence as far as the resonant characteristics of the two organs are concerned.

DISTORTION IN THE EAR

Distortion in the ear is reflected in perception as overtones and combination tones, which result from stimulation with sound waves of simple sine form. Helmholtz believed that the middle ear was the seat of aural distortion; however, persons who have lost the drum and the two larger ossicles of both ears are nevertheless able to hear combination tones (22, 114). After recording electrical responses from the round window of the cat, Wever and Bray (202) concluded that the inner ear, rather than the middle ear, is the chief site of distortion. Furthermore, cutting the tensor tympani muscle caused no notable alteration in the forms of the functions or the appearance of distortion.

RESPONSE OF SINGLE AUDITORY-NERVE FIBERS

Galambos and Davis (71) have recorded the response of single auditory-nerve fibers to pure-tone stimulation. They found that the auditory nerve responds even without acoustic stimulation, but that this spontaneous activity stops at the end of stimulation. Anesthetizing the end organ reduces spontaneous activity, and sectioning the nerve between the end organ and the recording electrodes abolishes it. Thus there is spontaneous discharge in the auditory afferents, as well as in other afferent nerves, when there is continuity with an active end organ. In addition, it was found that auditory nerves adapt to continuous stimulation of a constant intensity and thus resemble the pressure sense organs from which they are embryologically derived. Typically, both the unadapted and the partially adapted auditory fiber respond to an increase in stimulus intensity by increasing their rates of discharge. An auditory nerve fires at a maximum rate of 400 discharges per second and, when adapted, at about 100 to 200 discharges per second.

The range of frequencies which excites at minimal intensity is narrow for low-frequency fibers (700 cps) and broad for high-frequency fibers (7000 cps). Each fiber is "tuned in" sharply to a specific and narrow region of the sound spectrum. Galambos and Davis (71) reported they found no fibers with a characteristic frequency below 420 cps in the cat. However, the range of sound frequencies capable of exciting a fiber becomes more extensive as the intensity level is raised.

By varying frequency while holding intensity constant, it was found that the nerve-fiber discharge rate depends on both the frequency and the intensity of the stimulus.

Volley theories postulate a close relationship between sound frequency and nerve-discharge rate and, therefore, the frequency of nerve discharge should be either equal to the sound frequency itself or to some sub-multiple of it. Galambos and Davis (71), measuring the aural microphonic and nerve response, found that nerve impulses occur at a specific and particular portion of the sound-wave cycle. Although there is some variability in the spot on the aural microphonic cycle where the nerve impulse arises, the maximum variability amounts to about 0.25 millisecond. If we assume similar variability at other frequencies, it can be expected that the auditory nerve as a whole can discharge synchronously up to about 4000 cps.

Since each auditory fiber responds to only a narrow band of frequencies at minimal intensity, Galambos and Davis assume that each pure tone singles out and stimulates one particular and restricted region of the basilar membrane. Implicit in such a statement is the assumption that the peripheral endings terminate upon a small number of hair cells. Accepting such an assumption, Galambos and Davis conclude that a place theory of hearing is confirmed for pitch perception at the threshold, with different regions of the basilar membrane excited by different sound waves.

Action-Potential Threshold

Since the ear generates two types of electric responses to sounds (the aural microphonic in the cochlea, and the action potentials in the auditory neurons), it is difficult to determine the threshold of action potentials by frequencies (44, 47).

Davis et al. (46) found that the threshold of the aural microphonic is independent of the stimulating frequency from 1 to 5000 cps. They state that the auditory nerve's sensitivity to low tones is determined not only by the physical responses of the middle and inner ear, but also by the frequency-sensitivity that is interposed between the event that produces the aural microphonic and the initiation of the nerve impulse. They conclude that the aural microphonic is not a legitimate measure of the physiological sensitivity of the ear.

Davis, Fernandez, and McAuliffe (45), using high-frequency stimulation and suitably placed multiple electrodes in the guinea pig's cochlea, have found a third set of electrical waves. The summating potential adds the effects of two or more sound waves if they recur rapidly enough. It exists apart from the cochlear microphonic and the action potential of the auditory nerve. Thus we have the aural microphonic and a local excitatory potential as possible agents to initiate the neural response to sound.

Neural Inhibition: Acoustic Stimulation

Galambos and Davis (72) have reported marked inhibitory interaction between tones many octaves apart. Furthermore, the spontaneous activity of single auditory nerve fibers that cats show in silence can be inhibited by certain tones or noises. The tones which inhibit fall into one or more clearly defined inhibitory areas for each fiber, analogous to the response area which comprises the tones which excite the fiber.

Low tones have much more widespread inhibitory action on the activity aroused by high tones than the high tones do on low tones. Galambos and Davis (72) assume that the mechanism of inhibition is the spiral bundles of nerve fibers (116) which convey impulses from one region to another on the basilar membrane. Contrary to Steinberg and Gardner's (168) "line-busy" explanation of masking, Galambos and Davis explain masking as due to the masking tone's inhibitory effect on auditory nerve fibers.

Since a simple place theory assumes that a pure tone sets a restricted region of the basilar membrane into vibration, one would expect that a nerve fiber activated by one pure tone will be unaffected by a second pure tone so long as the two tones are sufficiently far apart in frequency. Galambos and Davis' results appear to contradict such an expectation.

Response of Auditory-Nerve Fibers: Tasaki

Tasaki and his associates have conducted more recent investigations to determine what kind of information individual nerve fibers carry from the ear to the central nervous system (178, 179, 180, 181). It has been shown that the basal turn of the guinea pig's cochlea responds to practically all frequencies in the audible range, while the upper parts of the cochlea respond only to low-frequency sounds (180, 181). Furthermore, when the response of the upper part of the cochlea has been eliminated, good normal responses can still be recorded in the basal turn. These results contradict any sharp localization of vibratory motion in the cochlea.

Tasaki (178), recording from the modiolus in the guinea pig, found that spontaneous discharges of impulses in individual auditory nerve fibers were never inhibited by acoustic stimulation. This finding contradicts results of Galambos and Davis (72), reported earlier. In addition, the nerve fibers arising in the basal turn of the cochlea respond to the tones of any audible frequency, while the upper part of the cochlea responds only to low-frequency tones.

Tasaki (178) concludes that, in the entire range of the audible sounds, the pattern of excitatory processes in the cochlea changes with frequency; the lower the frequency, the greater the shift toward the apical part of the cochlea. Thus a pure tone excites an area, not a spot, in the cochlea.

Tasaki and Davis (179), recording from the cochlear nucleus of the medulla oblongata, found that spontaneous impulse discharges were not inhibited by presenting a pure tone. In addition, they often encountered spontaneously discharging elements, some with rates as high as 200 per second. The rate of spontaneous discharge was increased by acoustic stimulation at the proper intensity and frequency, but the discharge was never inhibited.

These results differ from those of previous experiments (71, 72, 73) in the shape of the unit's response area and the behavior of the element's spontaneous discharge. One difference is due to the fact that the later studies used cats, while Tasaki and his associates had used guinea pigs. Also, the two groups of studies used different sizes of electrodes. Tasaki believes that his electrodes recorded axon responses and that Galambos and Davis had studied cell bodies. However, Tasaki's (178) observations were made chiefly with tones that were very brief, compared to previous studies, so the question of whether inhibitory effects might occur with longer-duration tones may still remain unsettled.

Three distinct conclusions can be drawn from Tasaki's work. First, the principal difference between auditory nerve fibers is in terms of what tones they respond to. A particular fiber may be activated by few, many, or (practically) all of the tones the animal may be expected to hear. Wherever the fiber's high-frequency limit is, its sensitivity drops very abruptly there; thus each auditory nerve fiber responds to all frequencies up to, but not beyond, its characteristic cut-off point. Tasaki concludes that this cut-off frequency is the neural counterpart of a corresponding cut-off in the mechanical motion of the basilar membrane, which he both observed directly and deduced from cochlear microphonic studies (180). Secondly, Tasaki's studies indicate that auditory afferents show only excitation, never inhibition, in response to stimulation. Finally, auditory fibers can be categorized into two groups on the basis of their response to intensity. One group of elements responds briskly to tones of moderate intensity, while another group reacts less rapidly. Tasaki believes that this indicates the fiber is connected to external or internal hair cells, respectively.

The studies by Galambos and Davis (71, 72) show that, at the cochlear nucleus, a tone possesses not only the capacity to activate certain neurons, but also the property of inhibiting the excitation of certain others. At the cochlear nucleus a tone increases activity at some frequencies, as well as decreasing or abolishing it at other frequencies. These separated regions of activity and inactivity may be a significant central cue to a tone's frequency.

Efferent Suppression of Auditory-Nerve Activity

Galambos (69) has demonstrated that stimulating the olivo-cochlear bundle reduces or abolishes the auditory nerve discharge to a weak or moderate click stimulus. Furthermore, even though anesthetizing and/or removing the middle-ear muscles and bones does not affect the phenomenon, it will disappear if the olivo-cochlear bundle is severed. Galambos concluded that, when the olivo-cochlear bundle is functioning, it suppresses the usual stream of auditory-nerve activity to normal acoustic stimuli.

Rasmussen (147, 148) has shown that the olivo-cochlear tract originates from cells near the superior olivary complex, ascends to the floor of the fourth ventricle, decussates, passes over the restiform body, and leaves the medulla with the contralateral vestibular nerve. The fibers then enter the Oort (cochleo-vestibular) anastomosis, pass into the modiolus, and are distributed as the mediolar spiral bundle in the cochlea. The ultimate peripheral termination of these fibers is still not definitely known.

In a series of experiments with electrical stimulation, Galambos and his associates failed to show what rostral brain structure connects with and activates the olivo-cochlear bundle (69). They also measured tones' thresholds in the presence of a masking noise with two normal cats, both before and after cutting the olivo-cochlear bundle. Since cutting the bundle at its point of decussation in the medulla did not change the thresholds, they concluded that the influence the efferent bundle has on the cochlea, if any, is not very important.

Desmedt and Mechelse (49, 50) have substantiated an acoustic centrifugal system, attempting to delimit for each frontal level in the brain the regions where stimulation will suppress acoustic input. They have found that the olivo-cochlear bundle does not cause suppression, but that the suppression effect is exerted within the cochlear nucleus. The results suggest that the phenomenon depends on activating descending fibers that have an inhibitory effect on nerve cells in the cochlear nucleus. Desmedt and Mechelse traced the centrifugal effect to the ventral and anterior aspects of the inferior colliculus and to the ventral nucleus of the lateral lemniscus. They have concluded that a specific extrareticular descending system of fiber connections is responsible for the cochlear gating.

Desmedt and Mechelse (51) found that the temporoinsular cortex sends corticofugal fibers to the extrareticular descending system, and it appears as if the beginning of the centrifugal system is found, not in the classical acoustic projection cortex, but in the more ventrally located "associative" cortex.

The idea that such inhibitory mechanisms might operate in the central nervous system is not new. Toennies (186) demonstrated that sensory inflow from the limbs of a cat is inhibited after spinal-cord stimulation. In addition, sensory information that enters the central nervous system undergoes substantial further modification in the central nuclei (82, 103). Therefore, it appears that the simple conception of the sensory pathway as one that delivers receptor events, unchanged, to the cortex appears untenable. With this in mind, we will now conclude our discussion of pitch perception by considering studies of the auditory pathway and auditory cortex.

If one assumes a place theory based on frequencies, the assumption's validity rests on finding a correlation between functional (frequency) specificity and specificity of anatomical projection. Studies of the auditory pathway have attempted to uncover a tendency to segregate frequencies at different fiber bundles. Most of the studies that will be reported deal with the response of the inferior colliculus and the medial geniculate body to a variety of stimulus conditions. If the results indicate that sounds are analyzed at the auditory cortex, they would substantiate frequency theory rather than place theory.

AUDITORY PATHWAY: INFERIOR COLLICULUS

Many investigations have shown that, throughout the mammalian series from rat to monkey, the auditory cortex is not necessary for hearing (performing learned responses to sound stimuli) (77, 120, 140). Such findings indicate that a subcortical acoustic center(s) connects with motor nuclei which mediate the response.

Kryter and Ades (106) have found that, in cats without auditory cortices, the inferior colliculus maintains approximately normal absolute-intensity thresholds. They concluded that the inferior colliculus is the primary subcortical reflex center.

Ades (3) has found that audible clicks produce strong responses in the superior colliculus. Accordingly, this must be the result of direct spread of activity from the inferior colliculus, since the auditory response of the superior colliculus is greatly diminished by cutting between the inferior and superior colliculi.

Severing the auditory pathway bilaterally below the inferior colliculi increased the cat's intensity threshold 40 dB. Ades (3) concluded that the inferior colliculus is a reflex mechanism for relatively simple auditory integration of conditioned responses to pure tones.

Ades and Brookhart (5) have shown that the inferior colliculus discharges via the superior colliculus into the bulbar and spinal efferent systems. Since animals can localize sounds in space without an auditory cortex, they suggest that the inferior colliculus, with its strong commisural connections and connections to efferent mechanisms, might be the principal integrative device for auditory localization.

Recording neural potentials at the inferior colliculus, Thurlow et al. (184) have found features similar to the response of elements at the level of the cochlear nucleus. Most noteworthy are the spike responses which are obtained at a given electrode position only for a certain band of frequencies, and in which the band width increases with intensity. Secondly, under continuous stimulation, adaptation occurs within a few seconds. This adaptation is more rapid than that which is found at the cochlear nucleus. Furthermore, Thurlow observed selective frequency masking of clicks. These results indicate that there is a spatial analyzing mechanism for frequency at the level of the inferior colliculus.

AUDITORY PATHWAY: MEDIAL GENICULATE BODY

Ades (1) failed to find strong connections between the medial geniculate body and any motor mechanism, so he concluded that this nucleus cannot be considered an important auditory reflex center. Papez (138) and Walker (192) have found degeneration of the medial geniculate body following temporary lobectomy. Thus it appears that the medial geniculate body is a relay center in the central auditory pathway, rather than a reflex center.

Ades, Mettler, and Culler (6) have demonstrated that small lesions in the medial geniculate body raise the absolute intensity threshold for stimuli of different frequency. The frequency affected depends on the lesion's location in the medial geniculate body.

Many studies have used microelectrode techniques to investigate the medial geniculate body's electrical response to auditory stimulation (1, 84, 153, 208). Gross and Thurlow (84), recording medial geniculate responses to tonal onset and click stimuli, have found that the responses are similar in form to those recorded at the inferior colliculus and the cochlear nucleus. Increasing the intensity of stimulation produces more responses of the same size, rather than increasing the size of the single responses. Adaptation occurs at this level, and at about the rate found at the level of the inferior colliculus. Furthermore, only certain frequencies cause the elements giving spike discharge to respond, which indicates specificity of response by frequency at this level of the nervous system.

Gross and Thurlow (84) have demonstrated masking the neural response to pure tones with noise and other pure tones. The neural response to clicks could also be masked. The click response was masked best by frequencies near the ones that produced the greatest neural response for a given electrode placement. This indicates responses in the auditory system are localized according to stimulating frequency.

Galambos et al. (74) have examined the electrical response aroused in the medial geniculate body by clicks. They found considerable variability in the response of single neural elements to a succession of identical clicks. This variability was reflected in the latency of response (6 milliseconds to 125 milliseconds), in whether or not the neural unit discharges, and in the number of discharges evoked by each click when the unit fired. They also observed spontaneous activity in single units. Apparently the medial geniculate body does not deliver impulses to the cortex promptly, as some studies have indicated (5, 31).

Galambos (67) has studied how single neural elements of the medial geniculate body respond to pure-tone stimulation. He found the band of frequencies that excites a neural unit was relatively wide at threshold values of the stimulus, and increased in width with an increase in stimulus intensity. Some units responded vigorously when the stimulus ceased but did not respond when a stimulus was applied. Furthermore, pure-tone stimuli were able to abolish the electrical response that a click evoked at the medial geniculate body. Low frequencies (particularly below 2000 cps) acted as inhibitors more frequently than high tones. Increasing the intensity of the tone relative to the click, increased the band of effective frequencies which inhibited the response to the click. The results obtained from pure-tone stimulation at the medial geniculate body do not indicate any clear and precise correlate for pitch in place of stimulation.

Katsuki (99) has recorded the response of single neurons to pure-tone stimulation from several levels of the auditory tract (cochlear nerve, cochlear nucleus, inferior colliculus, medial geniculate body, and the auditory cortex) in over 800 cats. He found marked spontaneous discharge of single neurons at the periphery, becoming less at higher neural levels. Furthermore, response areas at the periphery were quite wide for single neurons, and the higher the level, the narrower the area became. The narrowest area was found at the medial geniculate body, while wide response areas were obtained at the cortical level.

Katsuki (99) also found that a second tone could inhibit neural activity from a first tone when the second tone was very intense and fell within the frequency range the neuron responded to. This inhibitory phenomenon was observed throughout the auditory pathway, but most markedly in the peripheral region.

Katsuki and his associates also found that the thresholds of neurons in the reticular formation were higher than those in the classical auditory pathway. In addition, the number of neurons responding to tonal stimulation was relatively larger at the reticular system.

Katsuki concludes that complex sounds are analyzed as each auditory neuron's impulses in response to sound ascend to the cortex. The analysis begins in the cochlea and is completed at the medial geniculate body, since neurons have the narrowest response areas at this level. He believes the inhibitory interaction of neurons is the mechanism that narrows response areas at the higher levels of the auditory pathway. Finally, Katsuki concludes that the ascending reticular system is not concerned with the analysis of sound.

In summary, the studies reviewed indicate that a place principle analyzes sound at the higher levels of the auditory pathway. Furthermore, the findings of Kemp, Coppee, and Robinson (102) and Davis (37) indicate that neural activity becomes progressively less synchronized between receptor and cortex, thus placing serious limitations upon a volley principle of auditory analysis. The evidence seems to indicate that the centers of the auditory pathway are concerned with completing sound analysis and discriminating a sound's frequency.

Those interested in the comparative aspects of the auditory pathway will find the accounts of Kappers et al. (98) and Papez (137) valuable.

AUDITORY CORTEX

Most early studies of the auditory cortex have attempted to establish the location of cortical areas responsive to cochlear stimulation. (See Bremer and Dow (27) for a historical review of the problem.) Later studies have attempted to determine the neural organization within the classically known auditory areas.

Woolsey and Walzl (211), electrically stimulatingthe cochlear nerve in the spiral osseous lamina, found two responsive areas below the suprasylvian sulcus in the cortex. In auditory area I (A-I), lying on the middle ectosylvian gyrus, the base of the cochlea was represented in the rostral part, and the apex of the cochlear occupied the caudal part of the area. Auditory area II occupied the anterior ectosylvian, the pseudosylvian, and the posterior ectosylvian gyri. A-II was immediately ventral to A-I, and the order of cochlear representation was reversed.

Ades (2) recorded the activity that clicks induced in the cat's ectosylvian gyrus when strychnine was applied to the "primary" auditory area. He postulated a secondary acoustic (association) area, which included the basal cochlear region of Woolsey and Walzl's (211) A-II.

Tunturi (187), using tonal stimuli, clearly demonstrated frequency localization in the cortex of dogs. He doubted that auditory area II (211) was a single system, since he could not follow the frequency localization pattern from the anterior to the posterior ectosylvian gyrus. Furthermore, Tunturi (187, 188) defined a third acoustic area in the dog, separated from A-I and A-II, and lying beneath the anterior end of the suprasylvian gyrus.

Woolsey and Walzl (211) found that frequency representation decreases as one moves forward in the anterior ectosylvian gyrus, but Tunturi (189) and Hind (91) found exactly the opposite representation for this gyrus. Hind concluded that further research was needed to establish the functional unity of the anterior ecto-sylvian gyrus, as suggested by Woolsey and Walzl's use of the term A-II.

Bremer (26) has substantiated the secondary auditory area, that Ades (2) located on the posterior ectosylvian gyrus. He found the area was a narrow strip on the ventral border of the primary auditory area, coinciding with the "second auditory field" that Woolsey and Walzl described. Mickle and Ades (125) also found that the pseudosylvian and posterior ectosylvian gyri depend on corticocortical activation from A-I.

Rose (152) and Rose and Woolsey (153) studied the cytoarchitectural character-istics of the cat's auditory cortex and related them to evoked electric activity and to thalamic connections. Their chief problem was relating the basal end of A-II to the posterior ectosylvian area. They suggested reinvestigating A-II and its relation to A-I.

In 1953, Downman and Woolsey (54) re-examined the cochlear nerve projection to A-I and A-II-Ep (the posterior ectosylvian gyrus). They found that stimulating the basal end of the cochlea produced a high-frequency focus in the middle of A-II and another in Ep; this brought the physiological data into better accord with Rose's (152) anatomy of these parts of the original second auditory area. Downman and Woolsey also found long-latency responses in the posterior ectosylvian gyrus.

Downman and Woolsey's investigation also revealed that A-II and the posterior ectosylvian area receive afferent connections independent of the corticocortical connections from A-I. Kiang (104), using a cortical ablation technique, also concluded that activation of A-II and Ep is independent of A-I.

The secondary auditory area, as Woolsey and Walzl (211) originally conceived of it, does not seem tenable in light of present evidence. There seems to be frequency representation in the middle of A-II, although its order is the opposite of that in A-I -- a separated low-frequency anterior ectosylvian area -- and an isolated high-frequency Ep (posterior ectosylvian) region that has definite corticocortical connections from high-frequency A-I (54), but which can be activated by all parts of A-I (2, 4, 26, 104), as well as from the anterior ectosylvian low-frequency region (104).

Sindberg and Thompson (164) found a frequency representation of the cochlea in the posterior ectosylvian gyrus. The apex of the cochlea was represented ventrally, while the basal representation was more dorsal. This was the first experiment to examine the ventral Ep region during stimulation of the apical cochlear coil; the observed region extends below the limit of Rose's (152) posterior ectosylvian field.

Bremer (26) has reported the cat has a third auditory area lying near the anterior suprasylvian sulcus, adjacent to apical A-II, in Mickle and Ades' (125) polysensory area.

Loeffler (115), stimulating nerve fibers at the base of the cochlea electrically, found that an area in the insular cortex responded. He also found that stimulating apical fibers produced focalized responses in the ventral area of the insular cortex. Desmedt and Mechelse (51, 52) and Desmedt (48) have found that this area responds to both auditory and visual stimuli, and that visual and auditory responses interact. Desmedt and Mechelse have called this the fourth auditory area (A-IV).

In addition to all these areas that respond to acoustic stimulation, auditory responses have been recorded in still other areas of the cortex, even in the absence of the previously discussed auditory areas. For example, Buser, Borenstein, and Bruner (29) and Thompson and Sindberg (182) have recorded potentials in the suprasylvian gyrus of the cat. However, there was no evidence of frequency localization in this area.

Woolsey and Fairman (210) have noted responses to auditory stimulation in Talbot's visual area II, with a response latency of about 100 milliseconds. Bremer (26) also reported responses in this area.

In summary, we find that there are at least four complete representations for the cochlea, twice the number defined by Woolsey and Walzl. Frequency representation of the cochlea has been found in the suprasylvian fringe area, auditory area I, auditory area II, and the posterior ectosylvian gyrus. Furthermore, a much larger extent of the cortex responds to auditory stimulation than previously thought. However, the functional significances of the areas still remain to be determined.

Auditory Cortex Ablation Studies

To determine the functional significance of the cortical areas that respond to auditory stimulation, experimenters have studied how ablation of different areas affects auditory discrimination learning. (We will not be concerned with auditory localization following cortical ablation of the various auditory areas; however, the interested reader will find the studies of Neff et al. (33), Neff and Diamond (132), and Nauman (130) valuable.)

Cortical Ablations and Frequency Discrimination

After bilateral ablations of cortical areas A-I, A-II, and Ep (posterior ectosylvian gyrus), cats were able to perform frequency-discrimination tasks (30). However, Meyer and Woolsey (122) failed to demonstrate frequency discrimination in cats following bilateral ablation of A-I, A-II, and Ep. Goldberg, Diamond, and Neff (80) ablated areas A-I, A-II, Ep, and the cortex in the insular-temporal region; they found that cats could still learn to discriminate frequency changes. These studies used the training procedures described by Butler, Diamond, and Neff (30). Goldberg and Neff (78) have also found that frequency discrimination can be learned following bilateral removal of auditory areas A-I, A-II, Ep, and insular-temporal cortex. They concluded that the discrepancy between Butler, Diamond, and Neff (30) and Meyer and Woolsey (122) is due to differences in the way tonal stimuli were presented, rather than to the procedures used to condition the avoidance response. Goldberg and Neff (78) believe that animals deprived of auditory cortex will not learn a frequency discrimination when the neutral and avoidance tones are separated by a silent interval as much as a minute long. They propose a neural model describing the activity of subcortical auditory centers after ablation of auditory cortex. (See Neff (131) for a further explanation of this model.)

Mettler, Mettler, and Culler (121) removed a dog's entire cerebral cortex and found that the subject could still distinguish between two types of sounds. They established a conditioned reflex to a 1000-cycle tone, but the animal did not react to a bell of higher or lower intensity than the tone. The animal could not localize the source of the sound.

All of the previous studies that report frequency discrimination after removing various auditory areas of the cortex have used adult cats. Sharlock, Tucker, and Strominger (162) reported that large bilateral lesions in the auditory cortex of infant cats did not prevent them from learning a tonal-pattern discrimination; but adult cats with comparable damage did not acquire this discrimination. The authors concluded that neonatal damage to the auditory cortex appears to be less damaging than comparable damage at maturity.

Evarts (57) reported that almost complete removal of the auditory cortex does not permanently obliterate a habit learned preoperatively depending upon the subject's (a monkey's) ability to associate auditory (buzzer or silence) and visual (red or green light) cues. However, such a lesion does degrade the subject's ability to achieve a high level of accuracy.

Cortical Ablations and Pattern Discrimination

Diamond and Neff (53) have found that, after bilateral ablation of cortical areas (A-I, A-II, and Ep), cats cannot discriminate changes in temporal patterns of tones. Pattern discriminations likewise disappear after bilateral section of the brachium of the inferior colliculus or after bilateral removal of the insular-temporal cortex (79). Finally, Sharlock and Neff (161) have shown that ablation of areas A-I, A-II, Ep, and insular-temporal cortex completely destroys ability to discriminate changes in tone durations.

In summary, then, we find that bilateral removal of auditory areas A-I, A-II, the posterior ectosylvian gyrus (Ep), and the insular-temporal cortex -- all of which receive fiber connections from the medial geniculate body -- abolishes the ability to discriminate changes in temporal patterns of tones (53), changes in duration of tones (79), or to localize sounds (132). However, cats can learn to respond to changes in intensity (145) and in frequency (80) following similar ablations. We can conclude that the auditory cortex is essential to perform some -- but not all -- auditory discriminations. Furthermore, frequencies can be analyzed and discriminated at subcortical structures in the auditory pathway, particularly the medial geniculate body (99).

Some of the problems that exist in auditory physiology today are the delineation, function, and peripheral termination of the efferent auditory fibers. In addition, Galambos (70) has stated that for the past 75 years physiologists have been looking at neuro-neuronal contacts (synapses), excluding the possible significance of contacts between glial cells and neurons, and among glial cells. According to Galambos, the extensive presence of glial matter in the brain, spinal cord, and peripheral nerves -- as well as the observation that glial cells and neurons function together biochemically, so that neurons and glial cells constitute the functional metabolic unit of nervous tissue (97) -- argues that glial functions may play a role in several complexities of brain function. Determining the role and significance glial cells have in analyzing sensory information awaits further exploration and research.

Methodologically, further use of electrodes permanently implanted in the brain, and the peripheral auditory apparatus, will answer some questions about the neural effects acoustic stimulation has in the normal, waking organism. This technique can be used to evaluate the importance of attention, learning, and memory, and their relation to auditory problems.

Finally, further investigations into how the auditory neural system develops with age, together with comparative studies of auditory systems in fish through man, may indicate how much neural apparatus is necessary for pitch perception.

SUMMARY

In conclusion, we find that explanations for pitch perception have come a long way since the doctrine of "implanted air." New techniques have permitted the discovery of some of the mechanisms that the nervous system uses for the perception of pitch. However, the question of how a neural event is translated into perception still remains to be answered for all the sense modalities. Present evidence indicates that both a frequency principle and a place principle are involved in pitch perception.

Recently, there has been an increasing awareness of the central nervous system's importance in analyzing sensory information. Investigations have revealed the existence of an efferent auditory system. However, its role in pitch perception remains to be determined.

Finally, most of the experiments reported here have used pure tones, noise, or clicks as auditory stimuli. When investigating the physiology of the auditory system in animals, using auditory stimuli which are "natural" for the animal might reveal mechanisms for analyzing sounds that cannot be detected by standard laboratory stimuli. There might be a difference in the neural activity (e.g., latency, magnitude, threshold of response) of certain neural structures when a cat is stimulated by the "bark of a dog" or the "squeak of a mouse," rather than the onset of a tone or the sound of a click. At the human level, a mother's apparent selective sensitivity to her infant's crying, or people's ability to detect and clearly perceive their names when mentioned in a noisy situation, are further examples of significant auditory stimuli. Furthermore, ethnological investigations might uncover certain natural auditory stimuli which are "significant" or "meaningful" to an animal (e.g., a cat); and these stimuli may produce differential neural activity reflecting the physiological processes of selective auditory perception. Presenting a "significant" stimulus might inhibit ongoing neural activity and result in a faster neural and behavioral response than a "nonsignificant" auditory stimulus. The work of Hernandez-Peon and his associates (90) appears to support such an assumption.

The experimental investigation of such a "significant-stimulus" hypothesis could use a classical conditioning paradigm. Briefly, presenting a specific tone continuously before feeding (appetitive) or shock stimulation (aversive) would produce a stimulus which has "meaning" to the experimental subject. Investigating the auditory neural responses physiologically, using chronic and acute preparations, to compare a "meaningful" stimulus with other "nonsignificant" auditory stimuli, might reveal neural mechanisms (e.g., neural inhibition) designed for the rapid processing of "significant" auditory information. Such an experiment might indicate that additional neural structures, not yet known to participate in auditory perception, are involved.

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